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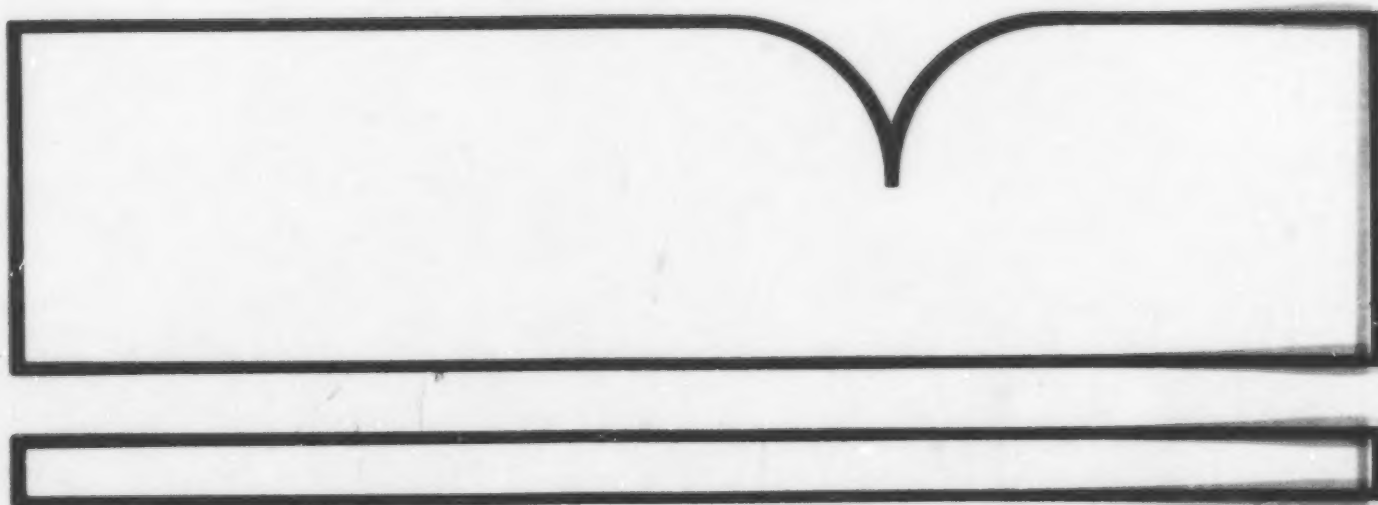
Effects of UV Radiation on Plants in the
Transition Region to Blue Light

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EFFECTS OF UV RADIATION ON PLANTS IN THE
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16. ABSTRACT Generalizations concerning the effects of UV radiation on plants are easy targets of criticism and certainly subject to considerable qualification. This review generalizes rather than presents a detailed compilation of available literature. Wavebands within the UV spectrum have been defined as UV-A, UV-B, and UV-C. Additionally, the terms near-UV (300-400 nm) and far-UV (200-300 nm) are often used. This synopsis emphasizes near-UV and concentrates on the UV-A waveband and its transitions to the blue and UV-B wavebands. Action spectra are used as a vehicle for presentation and generalization of UV effects on plants. The behavior of solar radiation is incorporated. Generalizations to emerge are: 1) Effects of UV-A radiation apparently involve many chromophores and interactions and none appears to be strictly specific to the UV-A; 2) qualitative differences in radiation responses are more apparent in the transition from UV-A to UV-B rather than in the transition between UV-A and blue light; 3) Solar UV-A behaves in a manner very similar to total solar radiation including the blue wave band, whereas solar UV-B is much more variable in nature; 4) with decreasing wavelength in the near UV, damaging reactions occur with increasing efficacy - these appear to operate by several different mechanisms; 5) protective effects mediated by UV-A radiation also occur.		
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Effects of UV radiation on plants in the transition region to blue light.

M. M. Caldwell

Generalizations concerning the effects of UV radiation on plants are easy targets of criticism and certainly subject to considerable qualification. Nevertheless, in this brief review I will generalize rather than to present a detailed compilation of available literature as has been admirably undertaken by Klein (1978). Other reviews on this subject are also available (Webb, 1977, Caldwell, 1971, 1981, Jagger, 1981). Wavebands within the UV spectrum have been defined as UV-A, UV-B, and UV-C as shown in Figure 1. Additionally, the terms near UV (300-400 nm) and far UV (200-300 nm) are often used. For perspective, the spectral irradiance received from common sources of UV radiation and some generalized absorption spectra for a few potential chromophores in plants are also portrayed in Figure 1.

This synopsis, as indicated by the title, emphasizes near UV and will concentrate on the UV-A waveband and its transitions to the blue and UV-B wavebands. Action spectra will be used as a vehicle for presentation and generalization of UV effects on plants. The behavior of solar radiation will also be briefly incorporated in this overview. Generalizations to emerge are: (1) Effects of UV-A radiation apparently involve many chromophores

and interactions and none appear to be strictly specific to the UV-A, (2) Qualitative differences in radiation responses are more apparent in the transition from UV-A to UV-B rather than in the transition between UV-A and blue light, (3) Solar UV-A behaves in a manner very similar to total solar radiation including the blue waveband; whereas, solar UV-B is much more variable in nature, (4) With decreasing wavelength in the near UV, damaging reactions occur with increasing efficacy--these appear to operate by several different mechanisms, and (5) Protective effects mediated by UV-A radiation also occur.

The transition from the blue waveband to UV-A is generally considered to be marked by two major biological phenomena, i.e., the lower wavelength limits both of human vision and photosynthesis of higher plants. However, there is no basic photochemical lower limit at 400 nm for these phenomena. Just as the inability of the human eye to see UV is limited by UV absorption of the lens, the ability of higher plants to carry on photosynthesis in the UV appears to be limited by absorption of UV in the epidermis. Without the epidermis, higher plant photosynthesis can be driven by UV just as photosynthesis of algae responds to UV (Figure 2).

Action spectra of many plant responses which might be termed regulatory in nature are presented for the UV-A waveband in Figure 3. Those have been normalized to the peak response within

the UV-A waveband. While this is hardly a comprehensive summary, it does convey the diversity of spectral response and behavior in this waveband. None of these responses is specific to UV-A since all of these spectra continue into the blue or UV-B. Of course, the classic "blue-light" responses, represented in this Figure by spectra for chlorophyll formation in Chlorella and carotenoid synthesis in Neurospora, include a significant response to UV-A.

Damaging photoreactions in the near UV can involve several chromophores and mechanisms. Yet, all have the common property that the quantum effectiveness of these reactions increases with decreasing wavelength (Figure 4). These spectra shown in Figure 4 have been selected to represent different modes of damage such as protein carrier inhibition, inactivation of ATPase, nucleic acid damage and loss of membrane selectivity. (However, none of these photoreactions involve exogenous sensitizing agents.) In the far UV, most of these damaging photoreactions exhibit still greater quantum effectiveness. Demonstration of damaging photoreactions in the UV-A is comparatively recent. Earlier work had largely discarded UV-A as effective in damaging photoreactions, especially for nucleic acids (Webb, 1977). Although the quantum effectiveness declines by orders of magnitude, UV-A is effective in producing both pyrimidine dimers and single strand chain breaks of DNA. However, the ratio of these lesions shifts with increasing wavelength so that the proportion of dimers formed

decreases much more abruptly than the incidence of chain breaks (Webb, 1977).

The differences between UV-A and UV-B induced photoreactions are not merely quantitative, there are also several qualitative differences: (1) The action spectra for lethality, mutagenic events and DNA breaks always exhibit a discontinuity or shoulder in the curves at approximately 330 nm in a variety of biological systems. This has been interpreted as indicating radical changes in the mechanisms of photoreaction between UV-B and UV-A although these mechanisms have not yet been identified (Kubitschek and Peak, 1980). (2) Lethality caused by UV-A has been reported to be strongly enhanced by oxygen for a number of different microorganisms whereas at shorter wavelengths in the UV-B and UV-C, lethality is largely independent of oxygen (Webb, 1977). (3) Molecular repair systems exist which can correct damage to nucleic acids caused by either far or near UV. Some of these repair systems are themselves induced by UV radiation, however, this induction of repair systems appears to be caused only by UV-B and UV-C and not by UV-A radiation (Menezes and Tyrrell, 1982). (4) Membrane damage induced by UV radiation at wavelengths greater than 310 nm contributes significantly to lethality of E. coli; however, at wavelengths shorter than 310 nm UV-induced membrane damage appears not to play a role in lethality of E. coli (Kelland et al., 1983).

Although UV-A radiation may not be effective in inducing certain nucleic acid damage repair systems, it is important in driving a specific process termed indirect photoreactivation. This is an enzyme-mediated system that repairs specific lesions, namely pyrimidine dimers, which can be caused by either near or far UV (Jagger et al., 1969). There are several other nucleic acid repair systems which do not require radiation and are, thus, termed dark repair systems (Smith, 1978). Another process induced by UV-A is termed photoprotection, a phenomenon by which near UV administered before inactivating UV will reduce the effect of the damaging UV. This operates primarily by delay of growth which allows normal dark repair systems, which are comparatively slow, to have more time to repair UV damage. A recent action spectrum for photoprotection and an action spectrum for photoreactivation are shown in Figure 5.

Flavonoid pigments are selective filters for UV and they can attenuate damaging UV before it reaches sensitive targets within plant tissues (Caldwell et al., 1983). These pigments can be induced by UV radiation in some plants as indicated by the action spectrum in Figure 5 (Wellmann, 1983). Although carotenoids absorb principally in the visible portion of the spectrum, their presence in plant tissues can reduce oxygen-dependent UV-A damage as indicated by an action spectrum for carotenoid protection in Figure 5. Quenching of singlet oxygen has been proposed as a

mechanism for this protection (Webb, 1977).

Thus, near UV can cause damage, it can induce certain repair systems to reverse UV-induced damage, it can drive the photoreactivation process, delay growth to allow dark repair systems to operate more effectively, and it can also cause direct damage to the repair systems themselves. Damage by UV can operate by several basic mechanisms as can the protective processes. Regulatory phenomena in the near UV also involve several chromophores and mechanisms.

Most of the photobiology of near UV is the result of laboratory study and often with monochromatic UV. To extend the knowledge of photobiological and physiological processes to a consideration of solar UV radiation effects on plants in nature involves another order of complexity. Not only is one dealing with polychromatic radiation with the attendant interactions between UV-induced phenomena, but also the solar UV spectrum undergoes considerable change, especially in the UV-B component of sunlight that reaches the Earth's surface. Figure 6 portrays the change in solar spectral irradiance along with the action spectrum for biological damage associated with DNA damage (a generalized spectrum from Setlow, 1974) and a photoreactivation spectrum. In the waveband where solar spectral irradiance is declining by orders of magnitude, the DNA damage response is increasing by orders of magnitude. Even if one assumes that there

are no interacting effects of different wavelengths, a quantitative evaluation of the potential of solar radiation to cause damage depends on the reliability of the damage action spectrum. Even though all action spectra associated with different modes of UV damage (Figure 4) decline with increasing wavelength, the rates of decline differ considerably and this greatly influences the assessment of the damaging effects of solar radiation (see Caldwell, 1981, for further discussion).

Flux densities of solar UV-A radiation per unit wavelength are of about the same magnitude as in the blue waveband (Figure 6). Furthermore, UV-A is not influenced by atmospheric ozone absorption and behaves in a manner similar to the blue waveband and to total solar shortwave radiation. The UV-B waveband, however, is much more variable since it is influenced by atmospheric ozone concentration and also undergoes greater changes as a function of solar angle (Caldwell, 1971, 1981). This is illustrated in a comparison of solar radiation measured over a latitudinal gradient ranging from Northern Alaska at sea level to the Andes at elevations of 3,000 to 4,000 m. Over this latitudinal gradient prevailing solar angles, atmospheric ozone concentrations and total atmospheric thickness vary considerably. Yet, at the time of year of maximum solar radiation, total solar shortwave radiation is similar at different locations along this gradient. In contrast, a comparison of the solar UV-B flux,

weighted according to its effectiveness to cause DNA damage, undergoes very large changes--a full order of magnitude (Figure 7). Also it is only the UV-B portion of the spectrum that would be influenced if the Earth's atmospheric ozone layer were to be reduced. Thus, the transition from UV-A to UV-B for solar spectral irradiance in nature is represented by large quantitative differences which do not occur in the transition between the UV-A and blue wavebands. It is also in the transition between the UV-B and UV-A where qualitative, and often quantitative, changes in the nature of photobiological effects also occur rather than in the transition from UV-A to blue light.

Acknowledgements

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Figure Legends

Figure 1. Spectral irradiance at 30 cm from three common UV lamps, solar spectral irradiance before attenuation by the Earth's atmosphere (extraterrestrial), and as would be received at sea level at midday in the summer at temperate latitudes. The absorption spectra of some common potential UV chromophores in plants are also represented: abscisic acid, ABA, is represented by the same curve as for nucleic acids; indoleacetic acid, IAA; the two forms of phytochrome, P_{fr} and P_r ; and general absorption spectra for flavoproteins and proteins. Major subdivisions of the ultraviolet spectrum are indicated. As originally defined UV-C is UV radiation less than 280 nm, UV-B is 280 to 315 nm, and UV-A is 315 to 400 nm; however, 320 nm is now more commonly used as a division between UV-B and UV-A. The near UV is commonly defined as 300-400 nm. From Caldwell, 1981.

Figure 2. Photosynthetic action spectra of a higher plant leaf, Brassica oleracea, with and without the epidermis (adapted from McCree, 1981) and of two algae, the green alga Ulva lactuca and the red alga Trailliella intricata (adapted from Halldal, 1967).

Figure 3. Plant action spectra in the UV-A waveband involving regulatory phenomena. Asterisks indicate photoinduction of carotenoid biosynthesis in Neurospora crassa (DeFabo, et al.

1976); open diamond symbols represent chlorophyll formation in Chlorella protothecoides (from Oh-hama and Senger, 1978); solid diamond symbols represent phototropic bending in Phycomyces (Galland, 1983); open circles represent the induction of seed germination in Lactua sativa (Wagne, 1966); filled circles represent unfolding of leaves for Triticum (Wagne, 1966); open triangles represent alterations of crown gall tissue culture growth of Parthenocissus tricuspidatus (Klein, 1964); solid triangles represent induction of protoplasmic streaming in Avena (Bottelier, 1934); solid squares represent stimulation of respiration in chlorophyll-free tissues of Solanum and Acer (Montfort and Rosenstock, 1950); open squares represent induction of chloroplast movement in Mougeotia (Haupt, 1959).

Figure 4. Near UV action spectra of plants representing basic modes of damage to plant tissues. Filled circles represent inhibition of Hill reaction activity in isolated chloroplasts of spinach (Jones and Kok, 1966); open triangles represent inhibition of adenosine triphosphatase from plasma membranes of Rosa damascena (Imbrie and Murphy, 1982); open circles represent induction of single strand breaks of Bacillus subtilis DNA (Peak and Peak, 1982); solid triangles represent lethality of stationary phase cells of E. coli associated with cell membrane damage (Kelland et al., 1983); open squares represent inhibition of alanine uptake in E. coli linked to inactivation of carrier

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proteins (Sharma and Jagger, 1981); closed squares represent inactivation of stationary-phase cells of E. coli associated with nucleic acid damage (Webb, 1977).

Figure 5. Action spectra for phenomena that ameliorate UV radiation damage in plants. Filled circles represent photoreactivation of stationary-phase E. coli (Jagger et al., 1969); solid squares represent growth delay (photoprotection) of E. coli (Kubitschek and Peak, 1980); open circles represent induction of flavonoid pigments in cell cultures of parsley (Wellmann, 1983); and open squares represent carotenoid protection of Sarcina lutea (adapted from Webb, 1977).

Figure 6. Relationship between solar spectral irradiance and a generalized action spectrum for DNA damage (from Setlow, 1974) and photoreactivation (adapted from Jagger et al., 1969).

Figure 7. Total solar shortwave irradiance at the time of maximum solar radiation at three locations in a latitudinal gradient in the arctic-alpine life zone from northern Alaska to the Andes of South America and solar UV-B radiation weighted for DNA damaging effectiveness based on the action spectrum of Setlow (1974) for the same locations (adapted from Caldwell et al., 1980).

References

- Bottelier, H. P. 1934. Ueber den Einfluss aeusserer Faktoren auf die Protoplastastroemung in der Avena-Koleoptile. Rec. Trav. Bot. Neerl. 31:474-582.
- Caldwell, M. M. 1971. Solar UV irradiation and the growth and development of higher plants. p. 131-177 in A. C. Giese, ed., Photophysiology. Vol. 6. Academic Press. New York.
- Caldwell, M. M. 1981. Plant response to solar ultraviolet radiation. in O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler eds. Encyclopedia of plant physiology, Vol. 12A Physiological plant ecology I. Responses to the physical environment. Springer-Verlag, Berlin. pp. 169-198.
- Caldwell, M. M., R. Robberecht, and W. D. Billings. 1980. A steep latitudinal gradient of solar ultraviolet-B radiation in the arctic-alpine life zone. Ecology. 61:600-611.
- Caldwell, M. M., R. Robberecht, and S. D. Flint. 1983. Internal filters: Prospects for UV-acclimation in higher plants. Physiol. Plant. (in press)
- DeFabo, E. C., R. W. Harding, and W. Shropshire Jr. 1976. Action spectrum between 260 and 800 nanometers for the photoinduction of carotenoid biosynthesis in Neurospora crassa. Plant Physiol. 57:440-445.
- Galland, P. 1983. Action spectra of photogeotropic equilibrium in Phycomyces wild type and three behavioral mutants. Photochem. Photobiol. 37:221-228.
- Halldal, P. 1967. Ultraviolet action spectra in algology. A review. Photochem. Photobiol. 6:445-460.
- Haupt, W. 1959. Die Chloroplastendrehung bei Mougeotia L. ueber den quantitativen und qualitativen Lichtbedarf der Schwachlichtbewegung. Planta 53:484-501.
- Imbrie, C. W. and T. M. Murphy. 1982. UV-action spectrum (254-405 nm) for inhibition of K^+ -stimulated adenosine triphosphatase from the plasma membrane of Rosa damascena. Photochem. Photobiol. 36:537-542.
- Jagger, J. 1981. Near-UV radiation effects on microorganisms. Photochem. Photobiol. Vol. 34:761-768.
- Jagger, J., R. S. Stafford, and J. M. Snow. 1969. Thymine-dimer and action-spectrum evidence for indirect photoreactivation in Escherichia coli. Photochem. Photobiol. 10:383-395.

- Klein, R. M. 1964. Repression of tissue culture growth by visible and near visible radiation. *Plant Physiol.* 39:536-539.
- Klein, R. M. 1978. Plants and near-ultraviolet radiation. *Bot. Rev.* 44:1-127.
- McCree, K. J. 1981. Photosynthetically active radiation. in O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler eds. *Encyclopedia of plant physiology, Vol. 12A Physiological plant ecology I. Responses to the physical environment.* Springer-Verlag, Berlin. pp. 41-55.
- Menezes, S., and R. M. Tyrrell. 1982. Damage by solar radiation at defined wavelengths: involvement of inducible repair systems. *Photochem. & Photobiol.* 36:313-318.
- Montfort, C., and G. Rosenstock. 1950. Die Lichtatmungsreaktion des Protoplasmas und ihre Beziehung zur Qualitaet der Strahlung. *Z. Naturforsch.* 5b:171-173.
- Oh-hama, T., and H. Senger. 1978. Spectral effectiveness in chlorophyll and 5-aminolevulinic acid formation during regreening of glucose bleached cells of Chlorella protothecoides. *Plant Cell Physiol.* 19:1295-1299.
- Peak, M. J., and J. G. Peak, 1982. Single-strand brakes induced in Bacillus subtilis DNA by ultraviolet light: action spectrum and properties. *Photochem. Photobiol.* 35:675-680.
- Sharma, R. C., and J. Jagger. 1981. Ultraviolet (254-405 nm) action spectrum and kinetic studies of alanine uptake in Escherichia coli B/r. *Photochem. Photobiol.* 33:173-177.
- Smith, K. C. 1978. Multiple pathways of DNA repair in bacteria and their roles in mutagenesis. *Photochem. Photobiol.* 28:121-130.
- Setlow, R. B. 1974. The wavelengths in sunlight effective in producing skin cancer: a theoretical analysis. *Proc. Nat. Acad. Sci. USA.* 71:3363-3366.
- Wagne, C. 1966. Effect of UV light on lettuce seed germination and on the unfolding of grass leaves. *Physiol. Plant.* 19:128-133.
- Webb, R. B. 1977. Lethal and mutagenic effects of near-ultraviolet radiation. *Photochem. Photobiol. Rev.* 2:169-261.
- Wellmann, E. 1983. UV radiation in photomorphogenesis. in Shropshire, W., Mohr, H. (eds) *Encyclopedia of plant physiology.* Vol. 16. Springer-Verlag, Berlin. (in press)

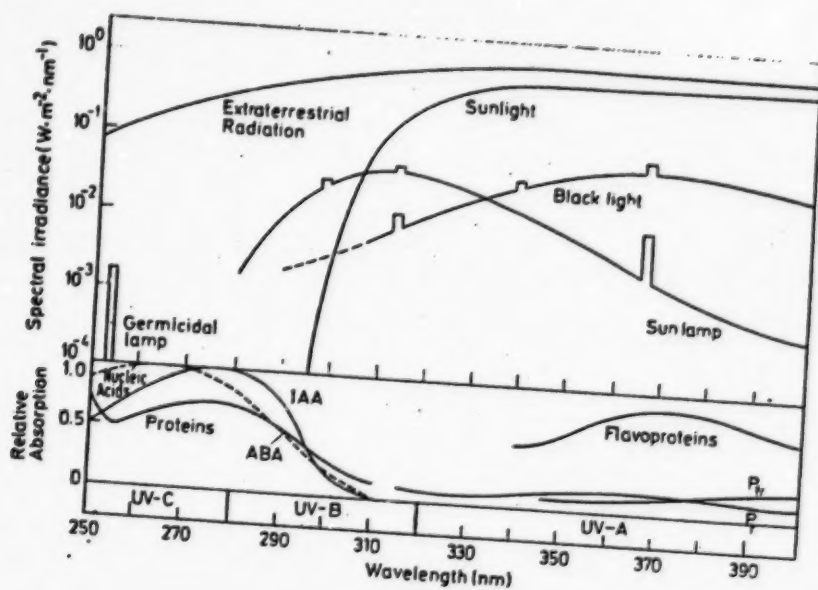


Fig. 1

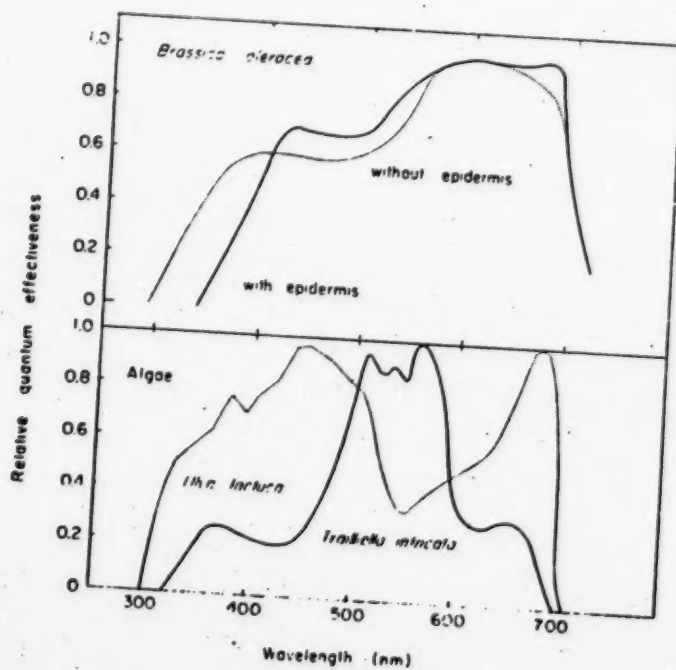


Fig. 2

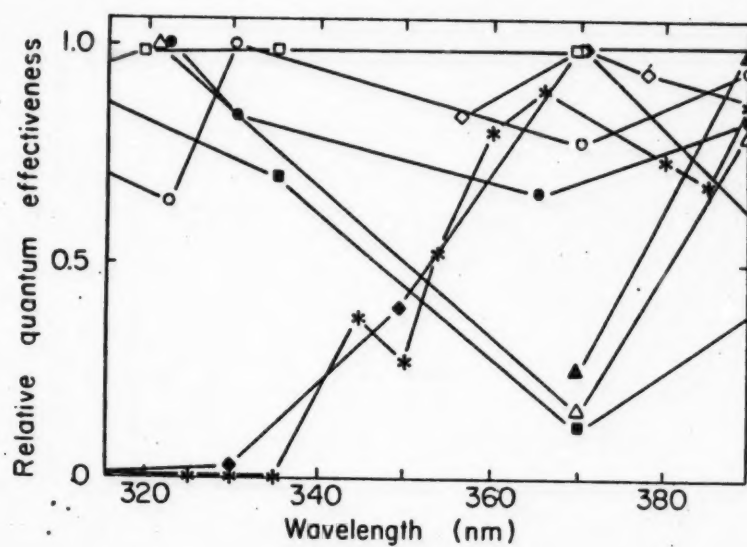


Fig. 3

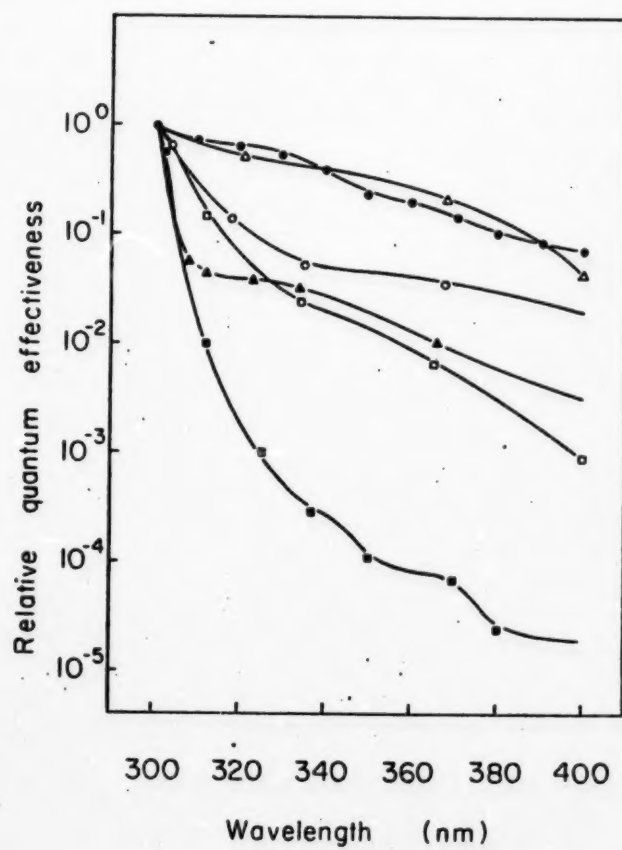


Fig. 4

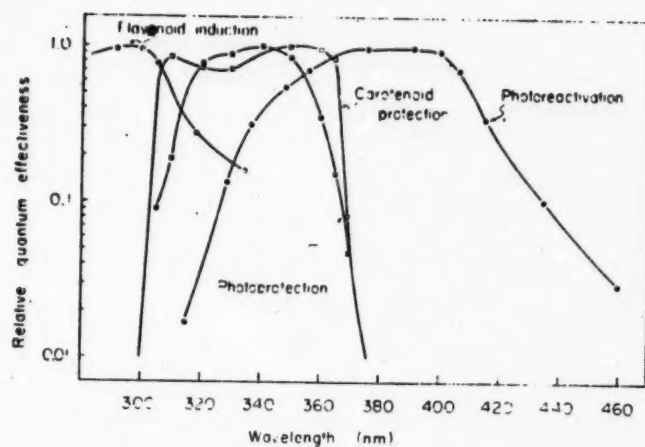


Fig. 5

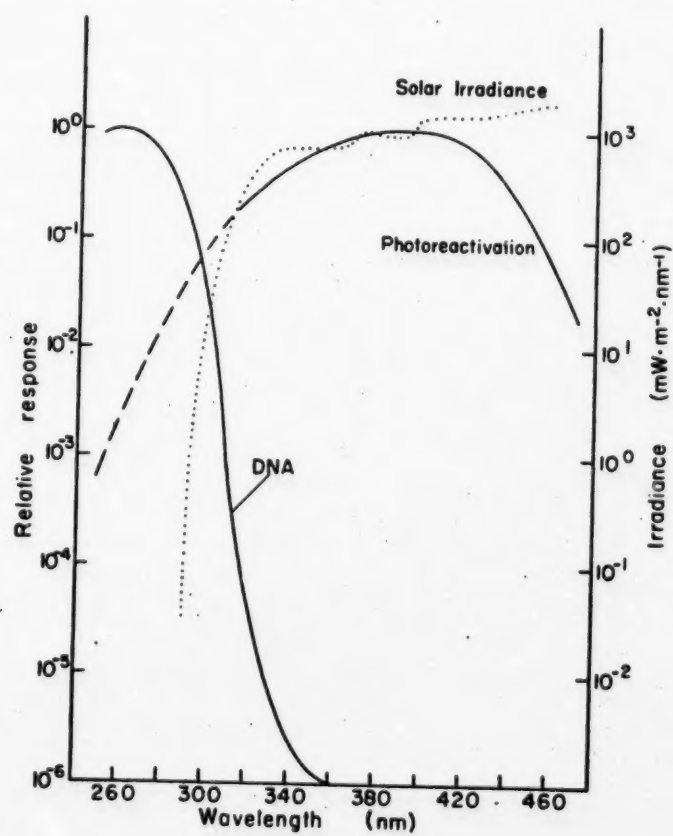


Fig. 6

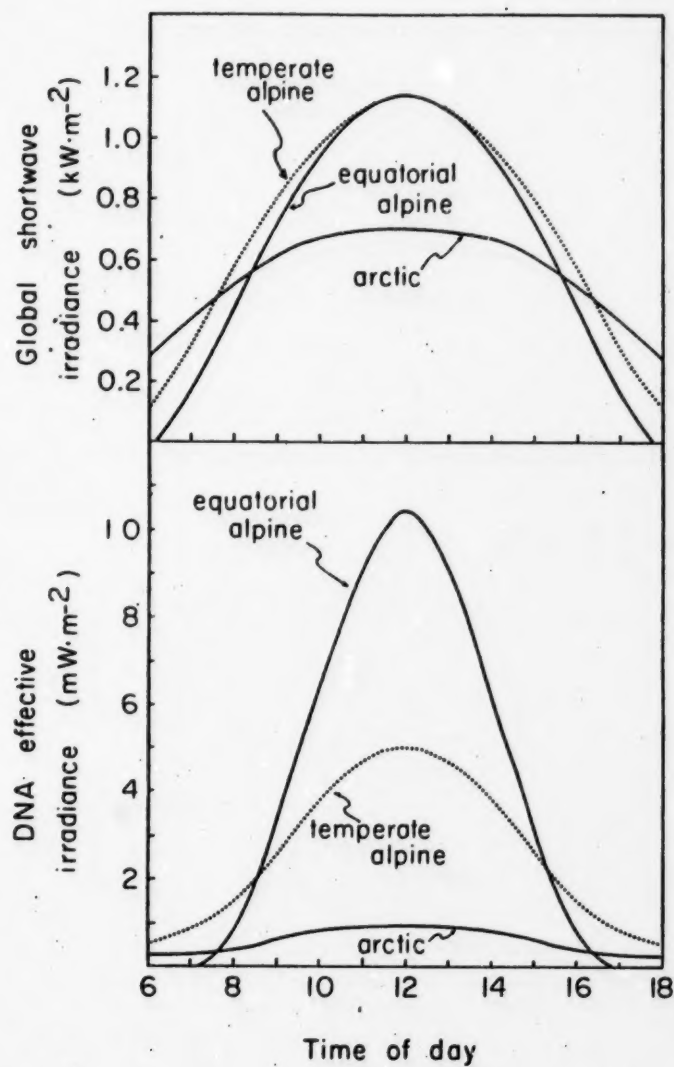


Fig. 7